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THE EAR OF MAN:

ITS PAST, ITS PRESENT, AND ITS FUTURE

BY

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NINTH LECTURE.[1]

THE EAR OF MAN:

ITS PAST, PRESENT AND FUTURE.

BY HOWARD AYERS.

THE study of the human ear, its structure and its functions, is not alone a *modern* endeavor on the part of man to "know" himself; for history tells us, that the Greek philosophers and anatomists sought, both by dissection and physiological experimentation, to ascertain the anatomy of the organ, and how it is that we hear by the ear. The extent of their knowledge we do not know, for most of their anatomical treatises are lost to us.

Empedocles, 473 years B.C., referred the perception of sound to the cochlea; and Aristotle (384 B.C.) was acquainted not only with the internal ear of the higher vertebrates, but with that of fishes as well.

The Egyptian school of anatomists does not seem to have progressed beyond the knowledge borrowed from the Greeks.

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[1] The memoir, of which this lecture is an abstract, will be issued in the *Journal of Morphology*, Vol. IV., No. 3.

At the present day we owe our knowledge of audition and its apparatus mainly to the French, German and Swedish anatomists of the past half-century. For notwithstanding the fact that the earlier Italian school had paid much attention to the auditory organ, they did not make any noteworthy contributions to our knowledge.

With all honor to the large number of workers in this field who have added facts from this side and that, and without whose labors it would have been far more difficult for the more recent writers to have accomplished their comparative studies and to have formed their generalizations, there are a few names among them which stand out in greater prominence than the rest, and to whose investigations we owe the facts which, when properly combined, furnish us with a solution of the problems of the origin of the ear and of its existing condition. They further allow us to predict with reasonable certainty the course which it will pursue in its further development. In other words, their investigations of the ear enable us to understand its past, its present and its future.

First among these names are those of C. Hasse of Germany and Gustav Retzius of Sweden, John Beard of England and E. P. Allis of our own country.

The two first mentioned have, by extended investigations into the structure of the adult condition of the internal ear of a large number of species, representing every important group of vertebrates, built up a comparative anatomy of the internal ear upon an anatomical basis alone. They have also given accurate descriptions and figures of the forms thus studied, which render possible the comparison of the embryonic conditions with the adult, and the establishing of important phylogenetic conclusions based on these relations.

John Beard first clearly saw the relation existing between the sense-organs on the surface of the body and the organ enclosed within the head by the formation of the auditory vesicle (the auditory labyrinth of the adult), but he failed to apprehend the *nature* of the involution and the relation of the sense organ to its walls.

E. P. Allis, by giving us the first thorough investigation of the relations of the sense-organs of the lateral line system to the surface of the body, in the account of which he describes the method of their enclosure within canals, the laws of their increase, and of the fusion and division of canals, the process of their sinking below the surface of the body, and of their enclosure within the cartilage (or the bone) of the skeleton,—made known the developmental plan according to which not only the superficial canal sense-organs grow and reach their adult relations, but also, as it is now discovered, the plan according to which the *ear sense-organ* divides and forms its canals and other parts. This latter fact is demonstrated by the published results of numerous embryological investigations on animals from the several classes of vertebrates.

In order that we may fully recognize the influence these investigations have had on the solution of the problems concerning the phylogenetic history of the human internal ear, it will be necessary first of all to understand the anatomy of the ear in some type form. For this reason I ask your forbearance while I briefly describe the internal ear of one of our American Torpedoes or Electric Rays (*Torpedo occidentalis*), and bring into comparison with it, part by part, the homologous structures of the ears of *Myxine*, or the Hag-fish, and Petromyzon, or the Lamprey Eel, as two representatives of the Cyclostome type; the Alligator as a representative of the reptilian type, the Thrush (*Mimus*) to illustrate the avian condition, and the ear of Man as typical for the mammalian group.

You will find the vertebrate internal ear described, in the text-books and special memoirs dealing with this organ, as a paired sense-organ, occupying a position on either side of the head behind the eye. It resembles in the general features of its relations to the head and nervous system the other organs of special sense. One prominent feature is its constant position between the roots of the fifth and tenth cranial nerves, which in the higher vertebrates especially, may be said to be pushed cephalad and caudad respectively by the growth of the ear.

The first trace of the ear seen in the embryo is, as shown in Fig. 7, a simple saucer-shaped depression of 8 the ectodermic epithelium on the dorso-lateral region of the head, not far removed from the gills. This thickened saucer sinks into the head, and divides into two parts, a superior and an inferior, or an utriculus and a sacculus as they are called. From the former the semicircular canals are differentiated, while the latter portion gives off the aqueductus vestibuli, or the endolymphatic duct, and the cochlear canal. These parts by further growth are converted into the *auditory labyrinth* of the adult.

Leaving out of consideration all other developmental processes connected with the completion of the auditory organ, such as its enclosure in mesodermic tissue which solidifies to form the ear-capsule (the bony labyrinth of the adult ear of higher forms), I wish to call your attention to two points of great importance for the correct understanding of the morphology of the ear.

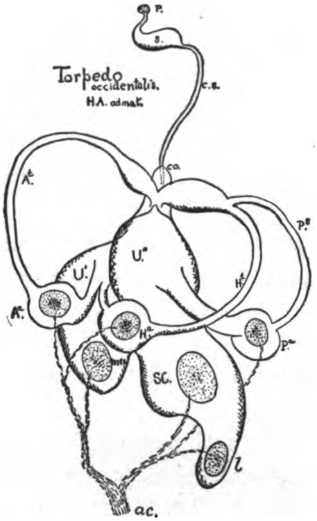

FIG. 1.—The left internal ear of *Torpedo occidentalis* dissected out of its cartilaginous capsule, and viewed from the outside. The somewhat diagrammatic figure represents the ear about twice its natural size, as found in a fish five feet in length.

A^a	Anterior ampulla.
A^t	Anterior canal.
ac	Auditory nerve.
c.e	Endolymphatic canal.
co	Utriculo-saccular cone.
H^a	External ampulla.
H^t	External canal.
mu	Macula utriculi duct.
l	Lagena and papilla lagenæ.
P	Surface pore of endolymph canal; *s* its sac.
P^a	Posterior ampulla.
P^t	Posterior canal.
SC	Sacculus and its macula sacculi.
U' and *U''*	Utriculus and utriculo-saccular chamber.

1st. The ear vesicle does not divide, as previous investigators have supposed, into superior and inferior portions, *but into an anterior and a posterior chamber.*

2d. The semicircular canals are not given off from the utriculus alone, but from the *sacculus as well.* With these two misconceptions corrected, the way is clear which leads to the really simple-as-the-truth account of the morphology of the vertebrate ear, and we shall never again encounter an *auditory labyrinth.*

An inspection of the Torpedo ear (Fig. 1) shows it to be composed of a number of more or less curved tubes, three of which approach a semicircular form, and have been on this account, since their discovery by Fallopius in 1561, called the semicircular canals. These three canals project from the central sac of the ear in three directions, and they lie approximately in the three planes of space. These planes do not coincide with the sagittal, horizontal and transverse planes of the body respectively, nor do the planes of any of the canals of the right side form continuations of the planes of the canals of the left side, or *vice versa.* The importance of these spacial relations will appear when we come to consider the physiology of the organ.

One of the canals projects forwards and outwards, and is known as the anterior vertical canal (the terms superior and sagittal canal have also been applied to it), another projects backwards and outwards, and is called the posterior vertical canal (the terms inferior and frontal have been given to it), while the third canal projects outwards and downwards nearly in the horizontal plane, and is called the external or the horizontal canal. Although it is usually stated in the text-books, that these canals occupy the three planes of space, and although, if not stated directly, it is none the less implied, that the canals also coincide with the three planes of the vertebrate body, — the sagittal, frontal, and horizontal respectively, — yet, we find that the very considerable and universal deviation from this hypothetical condition has been recognized by several investigators and the important bearing of the facts on auditory physiology at least in part recognized. I shall return to this further on.

Each of these canals opens into the main sac of the ear by its two ends, though this usual relation is not adhered to by all vertebrates, since some of the cartilaginous fishes show the posterior canal separated almost completely from the main sac, communicating with it only by a small, much reduced canal, the two ends of the semicircular canal having been brought together and its two terminal openings fused into one.

In Torpedo the proximal (superior) ends of the canals (Fig. 1, near *co*), are brought together and empty into a common but very short tube, which serves to maintain the communication with the main sac. Before uniting, however, the external and posterior canals unite by communicating with a common ama,[1] while the anterior canal swells out into an ama of its own. There is no constancy in the relation of the ends of the canals to each other or to the main sac, and, as we shall see later on, the matter has no great morphological or physiological importance. The enlargements at the proximal ends of the canals are found among most of the lower forms and occur in the *development* of the higher groups, usually disappearing before maturity is reached. The distal (inferior) ends of the canals are swollen into globular bodies, the ampullæ, which are usually flattened on one side by the entrance of the nerve branch, which breaks up into a brush of fine fibrils as it enters the ampullar wall. The nerve fibrils are distributed to the sensory cells of the crista acustica or transverse ridge, which projects from the bottom of the ampulla into its cavity and bears on its free surface the hair-bearing sensory cells constituting the percipient elements of the nerve end-organs of the ear.

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[1] I shall call the superior terminal enlargements of the semicircular canals amæ, from the Greek *ama*, — a water-vessel, — since, unlike the ampullæ or the inferior terminal enlargements, they contain no nerve end organs and are mere fluid-holders. Their significance is unknown to us.

Each ampulla is connected with the main sac by a shorter or longer tube (Figs. 1–6), the length of the tubes varying with the canal, and in greater degree with the animal species under consideration.

In the Torpedo the ampullar tubes of the anterior and the external canals join before opening into the utriculus (Fig. 1, near *U'*), while the posterior canal has a separate and very large tube which opens into the saccular division of the main sac (Fig. 1, near *U''*).

So far as the main sac of the Torpedo ear is concerned, it appears when viewed from the side (Fig. 1) to be composed of three large communicating chambers,—*U*,' *U*,'' and *SC*. When, however, it is seen from the inside, the chamber *U''* appears as a median vesicle from which are given off cephalad the utricular recess *U*,' and caudad the saccular recess *SC*, and the lagena. This central portion, then, is the connecting chamber of the primitive ear-sac, and is composed in part of the original sacculus and in part of the original utriculus. This chamber, as you see, is produced into a conical body, *co*, which is continued outward to the surface of the body by the long and slender canal *c.e.* Shortly before the slender tube or endolymphatic duct reaches the surface it presents an enlargement in the form of a broad sac which lies just below the skin of the dorsal region of the head. The duct is continued beyond the sac where it pierces the skin, and thereby places the cavity of the ear in communication with the surrounding medium. This duct communicates with some of the sense-organ canals lying in the skin, and is innervated by one of their nerves.

The sense-organs, six in number, with perhaps a trace of a seventh, are placed, three in the ampullæ of the semicircular canals, as already described, these being designated the cristæ, while the other three are known as the maculæ and papillæ acusticæ; the one in the recessus utriculi, *U*,' being the utricular macula *mu*, while the one in the saccular recess *SC* is called the macula acustica sacculi. It has budded off the lagenar spot, or papilla acustica lagenæ, *l*.

These organs are derived from the division of a single parent organ, as we shall see later, and hence their differences of form are secondary. The trunk of the auditory nerve (Fig. 1, *ac.*) is composed of two branches, each of which gives off three branchlets to the anterior and posterior divisions of the ear respectively. We may thus speak of an utricular and a saccular branch, each supplying the structures belonging to (*i.e.* developed from) its part of the ear. In Torpedo the anterior branch or the ramus utriculi gives off one branchlet to the crista of the anterior ampulla, another branchlet to the crista of the external ampulla, and a third to the macula utriculi. This latter branchlet is in reality composed of several branchlets; for the macula utriculi is a compound sense-organ, as the sequel will show.

The posterior or saccular branch gives off one branchlet to the crista of the posterior ampulla, a second branchlet to the macula sacculi, and a third to the papilla lagenæ, while there is possibly a fourth given off from the ampullar branch to an abortive ampullar organ for which Retzius proposed the name of *macula neglecta.* In the figure of the Torpedo ear this organ would lie in the ampullar tube of the posterior canal about where the horizontal canal crosses it, and its nerve would be in the figure entirely hidden from view.

Both Hasse and Retzius, after many years spent in the comparative study of the internal ear, have decided that between the ears of the *Cyclostomata* and the vertebrates of the *gnathostome* type there was no discernible basis of homology. The gulf separating the two types prevented the recognition of such genetic relationships as might exist. Since my studies lead to a very different conclusion, a short account of the salient features of the Cyclostome ear, introduced here, may serve as a preliminary to the consideration of the morphological laws governing the development of the vertebrate ear, alike in its ontogeny and its phylogeny.

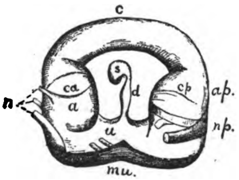

FIG. 2. — The right internal ear of the Hagfish (*Myxine glutinosa*), seen from the inside or cerebral face. Figure after G. Retzius. The figure represents the ear somewhat enlarged, and does not show the shape or exact positions of the contained sense-organs.

a	Anterior ampulla.	*d*	Ductus endolymphaticus.
ap	Posterior ampulla.	*mu*	Macula utriculi et sacculi.
c	Anterior and posterior canals.	*n*	Nerve branchlets.
ca *cp*	Ampullar ends of the same.	*u*	Utriculo-sacculus.
		s	Sacculus endolymphaticus.

The internal ear of *Myxine* (Fig. 2) is the simplest known among vertebrates. It is divided by a vertical line passing through the letter *c*, the sac of the endolymphatic duct (*s*), and the duct itself into two quite symmetrical portions. The anterior corresponds to the anterior part of the Torpedo ear, and there is a similar correspondence between the posterior halves of these two ears. The main points of difference are, 1st, The sense-organs of the Myxine ear are only three in number, or at most four. 2d, The canals, only two in number, and they do not communicate by their amal ends with the main sac of the ear, or the utriculo-sacculus, for here the chambers are not separated though distinctly marked off. 3d, The endolymphatic duct does not communicate in the adult with the surface of the body.

The auditory nerve, however, has the same number of divisions, — two, — and they supply the utriculus with its anterior ampulla, and sacculus with its posterior ampulla, respectively, the same as in the Torpedo ear.

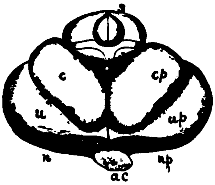

FIG. 3. — The right internal ear of a Lamper-eel (*Petromyzon fluviatilis*), viewed from its inner or cerebral face. The figure after Retzius.

ac	Auditory nerve.	*u*	Utriculus.
c	Anterior canal.	*up*	Sacculus.
cp	Posterior canal.	*s*	Ductus et sacculus endolymphaticus.
n	Ramus utricularis.		
np	Ramus saccularis.		

In *Petromyzon* the ear is much more compact than in any other known form; the canals, though two in number and well developed, do not rise above the surface of the utriculo-sacculus; and although they fuse together at their proximal ends as in *Myxine*, they also open into the main sac by a short, small tube. The whole structure is divisible by a vertical passing through the apex and the middle of its base into anterior and posterior divisions, and the parts thus separated are very much the same as in *Myxine*, showing but slight modifications of the floor of the sac in the direction of a differentiation of the sense-organs contained, and in the formation of chambers for the reception of the new organs thus budded off. Though slight, this change

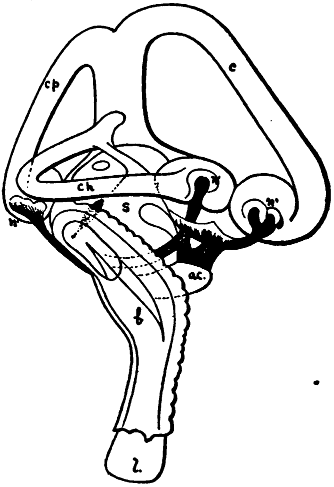

FIG. 4.—The right internal ear of *Alligator mississippiensis*, seen from the outer face. Figure after G. Retzius. The figure outlines do not bring out the relations of the parts distinctly, and only the more important parts are lettered.

ac	Auditory nerve.
b	Pars basilaris cochleæ auct.
c	Anterior canal.
ch	External canal.
cp	Posterior canal.
l	Lagena.
n'	Cristæ acusticæ of the ampullæ.
s	Sacculus.

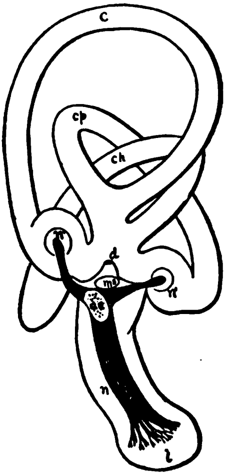

FIG. 5.—The right internal ear of *Turdus musica*, seen from the inner or neural face. Figure after G. Retzius. The letters are placed only on those parts of the organ plainly visible in the figure.

ac	Acoustic nerve.
c	Anterior canal.
ch	External canal.
cp	Posterior canal.
d	Ductus endolymphaticus.
l	Lagena.
ms	Macula sacculi.
n	Lagenar nerve.
n'	Cristæ acusticæ of the ampullæ.

is very important, for it introduces us to a series of changes which have led to the production of the gnathostome type of ear.

The reptile, bird, and mammal ears furnish us with a progressive series in which the parts already present in the Torpedo are carried to successively higher degrees of perfection. The most noticeable change from the Torpedo condition is the much elongated lagenar region, or, as it is called in the mammalia, the cochlea, which by means of the high differentiation of its contained sense-organ has risen to first rank among the auditory sense-organs.

The utricular and saccular regions are relatively much reduced. The semicircular canals have undergone a similar reduction, and among the birds and mammals appear more nearly semicircular or more evenly curved than in either the reptiles or the fishes.

All of these ears retain traces of the primitive division into anterior and posterior chambers, and the relation of the nerves described for the *Cyclostome* and the Torpedo obtains throughout the group, except, of course, where a given sense-organ has divided, when, as is frequently the case among the higher types, two or more nerve branchlets are present where only one existed in the lower type.

In Fig. 6, which is a figure of the developing human ear seen from the outside, the anterior and external ampullæ are intimately related to each other and to the utriculus *U*, while the posterior is given off from the sacculus. A line passed through the space between *U* and *S* of the figure, and continued so as to pass out just above the ampulla of the posterior canal, divides the ear into its anterior and posterior halves, which, owing to the distortion produced by the enormous growth of the cochlea, now appear as superior and inferior portions of the canal system of the ear.

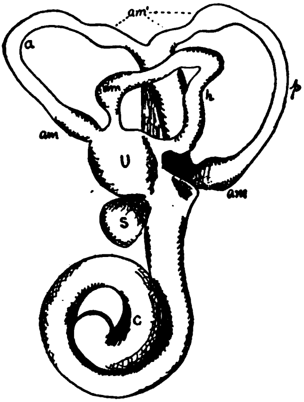

FIG. 6.—The left internal ear of a human embryo, 22 mm. in length, seen from without and below. Figure after W. His., Jr. The figure is from a model constructed from serial sections, and represents the ear much magnified.

a	Anterior canal.
am	Ampulla.
am'	Amæ. The middle reference line is superfluous.
c	Cochlea.
d	Ductus endolymphaticus.
h	External canal.
s	Sacculus in the restricted sense; really only the recessus sacculi.
u	Utriculus.

The development of the special sense-organs of the lateral line in *Amia* or the ganoid Dog-fish, as made known by Allis, gives us the key to the solution of the problem of the homologies of the parts of the internal ear. In this fish the inclosure of the canals and the formation of the pores and tubes, while it is undoubtedly the primitive process, is essentially a simple and regular process, and when it is fully carried out *the canals arise in separate sections, each of which contains a single sense-organ.*

In the young Dog-fish, in which the canals have not begun their development, the sense-organs lie below the surface and may be traced as more or less continuous whitish lines. "These lines mark general and extensive surface depressions." From the bottom of these general surface depressions the sense-organs sink down forming, as they do so, small pits, at the bottom of which the organ lies. The lips of the pit grow upward and inward, and, meeting above, arch over the pit forming the beginning of a canal. This arch grows away from the pit in two directions until it meets another canal, with which it fuses, or until its energy is spent, when it comes to a standstill and remains a longer or shorter canal open at both ends, possessing somewhere near the middle of its course the canal sense-organ which gave the first impulse to the development of the canal. The sense-organ lies in a pit which represents what we know in the ear canals as the ampulla. The lateral line sense-organs are then supplied with, or lie in, ampullæ.

The canals being formed in short sections, one to each sense-organ, and fusing as they do to make longer canals, we should expect the compound canal at the point of fusion of its two components would retain a pore connection with the surface from which the canals were formed. Such is the case.

Again, in the division of a canal organ and its canal, we should expect to find the canal retaining its surface communication by means of a single pore, if the division did not progress to completion, and we find this occurs regularly in the development of canals. The reverse of this process also occurs, in which the pore divides first, while the parent canal may remain undivided.

We shall see later on that the ear canals fuse and retain their communication with the surface by means of a single pore, and that in one instance a canal organ divides, bringing about an incomplete division of the original canal, so that both canal organs communicate with the mother surface by means of a single pore. This is true in the case of the anterior and external ear canals of Torpedo (Fig. 1, *U'*). We shall also find that the division of a canal organ may be barren of result so far as the production of a separate canal is concerned, and that in this case the offspring may retain its position in the parent canal. As an instance of this condition in the ear we have the macula neglecta (Fig. 7, *ma*), which has arisen by the division of the parent organ, the primitive sense-organ of the posterior ampulla.

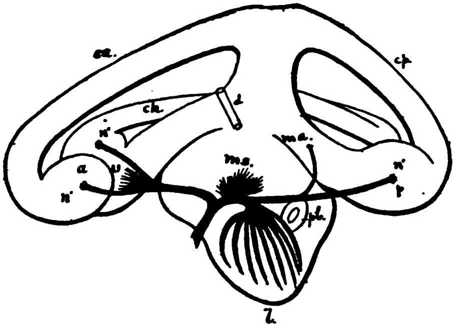

FIG. 7.—The right internal ear of the European Adder (*Tropidonotus natrix*), seen from the inside. Figure after Dr. Kuhn. This ear shows very distinctly the division into anterior and posterior chambers, especially in the arrangement of its sense-organs.

a	Anterior ampulla.	*ma*	Macula acustica neglecta of Retzius.
ca	Anterior canal.	*ms*	Macula acustica sacculi.
ch	External canal.	*n'*	Crista acustica ampullarum.
cp	Posterior canal.	*p*	Ampulla posterior.
d	Ductus endolymphaticus.	*pb*	Pars basilaris cochlear auct.
l	Lagena.	*u*	Utriculus.

The early history of the Elasmobranch auditory capsule does not differ materially from that of other forms except in the rate of growth.

In this respect it is a much more favorable object for the study of the development of the internal ear than any vertebrate with which I am acquainted. Fig. 8 shows the auditory involution after it has assumed the saucer-shape already alluded to. This condition is the result of a concomitant thickening and sinking of the ectoderm, which over the area of the saucer represents one of the canal sense-organs of the lateral line system, and the whole process from the beginning on is but a repetition of the formation of the canal organ and its canal, as sêen in *Amia*. As the saucer-shaped thickening sinks below the surface, the opening on the surface grows smaller, the bottom of the saucer increases in size, and the resulting structure is an auditory vesicle distinctly flask-shaped (Fig. 9, *a. v*). The neck of the flask grows longer, and finally appears bent backwards and inwards, owing to the increase in size of the head in this region, which causes a transla-

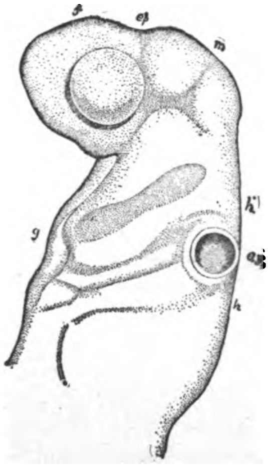

FIG. 8.—The head of an embryo Shark (*Acanthias vulgaris*), from nature, magnified 20 times. The figure shows the saucer-shaped depression containing the insinking sense-organ which is to be converted into the auditory sense-organs of the Shark.

a.v	Auditory saucer (vesicle).
ep	Epiphysis.
f	Fore-brain.
g	Gill region.
h, *h'*	Upper and lower hind-brain region.
m	Mid-brain.

tion of the auditory capsule forwards and outwards (Fig. 10, *d*).

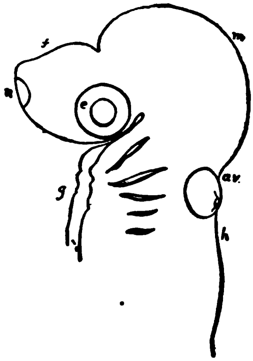

FIG. 9.—The head of the embryo smooth Dog-fish (*Galeus canis*), seen from the left side. Figure drawn from nature, magnified about 20 times. The flask-shaped auditory vesicle is shown prominently placed above the gill region. Letters as in the preceding figure.

a.v	Auditory flask.
e	Eye.
f	Fore-brain.
g	Gill region.
h	Hind-brain.
m	Mid-brain.
n	Nose.

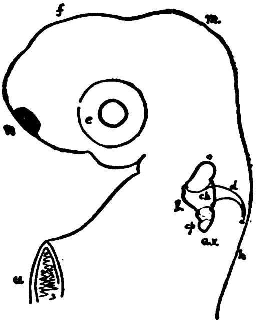

FIG. 10.—The head of an older Shark of the same species, viewed from the left side. The figure, which was drawn from the living fish, shows the internal ear well advanced in its development. The rudiments of the semicircular canals and lagena are seen pushing out from the auditory sack (respectively the utriculo-sacculus, which has sunk far below the surface, with which it is, however, still connected by its sickle-shaped ductus endolymphaticus).

a.v	Auditory vesicle.	*cp*	Posterior canal.
c	Anterior canal.	*l*	Lagena.
d	Ductus endolymphaticus.	*m*	Mid-brain.
e	Eye.	*h*	Hind-brain.
f	Fore-brain.	*n*	Nose.
ch	External canal.	*u*	Umbilical cord.

During this lengthening of the neck of the flask, which becomes the surface canal of the adult ear, the body of the flask is much changed in shape.

First of all, it becomes compressed laterally, and is then drawn out in an antero-posterior direction. During this process the anterior end comes to point outward, while the posterior end is directed inwards toward the median line. There may now be seen several changes in the shape of the vesicle which, while not conspicuous, are very important, since they usher in a succession of transformations which ultimately produce the three semicircular canals and the rudiment of the cochlea. These changes are visible on the outer and upper faces of the vesicle as slight ridge-like elevations of the surface, and on the posterior ventral end of the vesicle as a knob-like prominence (Fig. 10, *c*, *ch*, and *a.v*). Of the former there are two, of the latter a single one. The

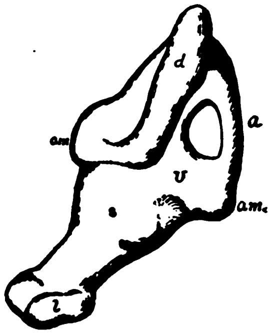

FIG. 11.—The ear of a very young Rabbit embryo, 11 mm. long. Figure after Krause.

a	Anterior canal.
am	Ampulla.
d	Ductus endolymphaticus.
l	Lagena.
s	Sacculus.
u	Utriculus.

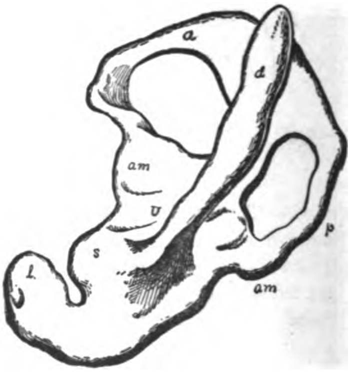

FIG. 12.—The internal ear of a somewhat older Pig embryo, 33 mm. long. Figure after Krause.

a	Anterior canal.
am	Ampulla.
d	Ductus endolymphaticus.
l	Lagena.
p	Posterior canal.
s	Sacculus.
u	Utriculus.

former structures seen from inside the vesicle are merely depressed grooves in the wall of the vesicle, and the latter a sunken but broadly open pit. These grooves grow deeper, their edges grow together, first, along the middle part of their course, thereby producing canals.

The lips of the pit fuse by reaching across the middle of the opening, and thus produce the beginning of the posterior canal, which, by its continued growth upward, soon reaches and fuses with the anterior canal. The terminal pores of these two canals, at what proves from later events to be their amal ends, fuse and open into the vesicle by a single pore.

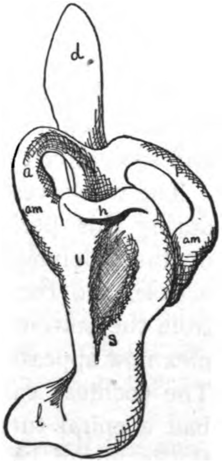

Fig. 13.—The left internal ear from a human embryo, 13 mm. long, about the fifth week of development.

a	Anterior canal.
am	Ampulla.
d	Ductus endolymphaticus.
h	External canal.
l	Lagena.
p	Posterior canal.
s	Sacculus.
u	Utriculus.

The introductory stages in the development of the human ear are but a repetition, as regards essentials, of the process as I have described it in the shark.

When fully cut off from the exterior, the auditory vesicle forms a compressed sac having an irregular quadrangular shape. This condition is found in embryos of three and a half to four weeks. The utricular and saccular divisions are readily distinguished, and even now the semicircular canals have begun to differentiate by the formation of two shallow depressions in the walls of the utriculus. Both the pocket common to the vertical canals and the pocket for the external canal are present. Below the latter is seen the larger and deeper evagination for the cochlea. When the embryo has reached the length of 8 mm., the cochlea has so far developed as to stand out distinctly from the sacculus, and is at the same time bent (Fig. 11, *l*). At both ends of the common pocket of the verticals, and at one end (anterior) of the external depressions, are slight enlargements — the future ampullæ. From now on, the parts rapidly acquire individuality. The anterior canal is completed first. Then the posterior becomes cut off, and soon after the external is perfected.

The whole vesicle undergoes a marked change in form during this period, for, owing to the growth of the ductus endolymphaticus from the apex of the primitive vesicle, and the great elongation of the cochlear tube from the bottom of the saccular region, the canal complex now appears drawn out in a dorso-ventral direction. The cochlear canal has now, about the fifth week, one half a spiral turn, and a long groove has appeared on the inside of its wall (fold on the outside), from which the nerve end-organ — Corti's organ — arises. In the embryo of 30 mm. (Fig. 6) length the canals are well formed, and the ampullæ are quite prominent. The two verticals which from *their mode of development have up to this time occupied the same plane*, now begin to diverge, and the planes of the canals now meet in the middle of the common tube which unites them. Their angle at this time is 150°.

This method of origin is most interesting and important in its bearings on the spacial relations of the adult ear canals. The cochlea has now made nearly a whole spiral turn. About the second month the internal ear has assumed the fœtal conditions, and its development from this point on consists in the perfection of the parts already marked out. The canals and ampullæ have acquired their adult characters, and the cristæ are distinctly formed, although the sensory cells have not acquired their mature structure. Each canal has at this stage a noticeable swelling at the opposite end from the ampullæ. In these you will recognize the amæ which I described in the fish ear as an adult characteristic. In the human ear the ama of the external canal is the only one usually persisting beyond the fœtal condition.

The cochlea has continued its development, and is readily seen in the greater number of spiral turns it has acquired, and the row of sense-organs, formed by the budding of the original cochlear sense-organ or papilla lagenæ, has now several hundred discreet sense-organs which are so closely related in structure and function as to pass as one organ, the organ of Corti.

One very important matter belonging with the anatomical facts I intentionally neglected, for, until we had gained a knowledge of the course of development of the ear as a whole, and of the details of canal formation in particular, we were not likely to fully appreciate its bearings on the problem of the inter-relation of the sense-organs of the auditory complex and of their canals. It is the morphological value of that sense-organ which, ever since its discovery by Retzius, has been such a source of discussion and investigation; viz. the macula acustica neglecta, supposed by some to belong to the utriculus; by others, to the sacculus in the older sense.

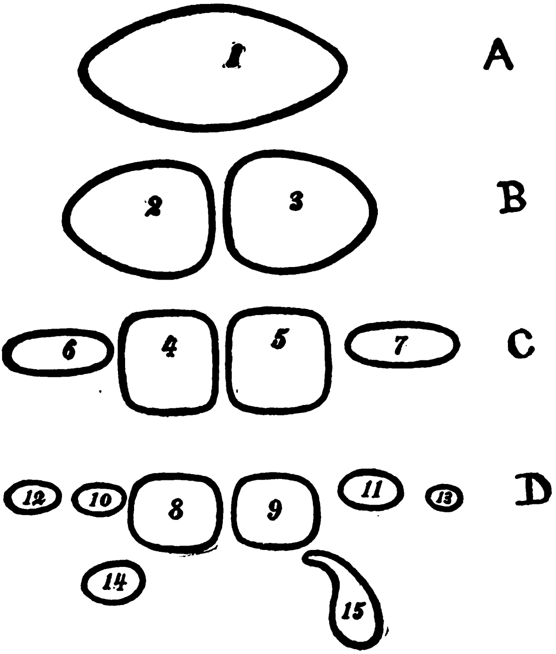

FIG. 14.

A Auditory vesicle.
B Utriculo-sacculus.
C Utriculo-sacculus + two ampullary canals.
D Utriculo-sacculus + two ampullary canals and lagenar canal.

Stage A represents the undivided superficial sense-organ of the vertebrate ancestor, as it is invaginated from the surface and enclosed within the auditory vesicle to function as the macula acustica vesiculi; the only auditory sense-organ of this stage. It is but little removed from the canal organs as they exist in, *eg.*, *Amia*, and differs from it mainly in size. This condition is not represented in the adult of living vertebrates.

Stage B represents the first division of the macula vesiculi, into its two offspring the maculæ acusticæ utriculi et sacculi. This stage is likewise not represented among living forms.

Stage C is so characteristic of the *Cyclostomata*, so far as we know them, that we will call it the Cyclostome stage. Here the cristæ acusticæ anterior et posterior have made their appearance.

Stage D shows the condition of the organs in the *Gnathostomata*, hence its name the Gnathostome stage. The cristæ acusticæ anteriores, horizontales, posteriores and abortivæ are all developed by the division of the two parent ampullary organs of the Cyclostome ancestral stage, while the maculæ utriculi et sacculi undergo division, giving rise to the parents of the utricular and saccular complexes of sense-organs. These latter reach their highest differentiation in some rodentia and porcine species.

Retzius finally came to the conclusion that this nerve-end organ had arisen from the posterior, ampullar sense-organ, and that among the higher forms, especially the mammalia, it was no longer produced, or, as he expressed it, the macula neglecta in these forms had disappeared in the crista acustica posterior.

After an examination of all the evidence bearing on this question, both from the embryological and the anatomical sides, I have solved the problem of the morphological value of the parts of the internal ear and their inter-relationships, by the discovery of the very simple law which governs their origin and succession. Let me give you the whole problem in a nutshell, even at the risk of some slight repetition.

The primitive auditory sense-organ is invaginated from the surface of the body, and may be said at this time to be in the vesicular stage (Fig. 14, *A*). So far as we know, this condition is not retained by any adult living vertebrate. And it is quite possible that the auditory saucer may contain the rudiments of the two primary sense-organs of the Cyclostome ear. The parent sense-organ soon divides transversely into two nearly equal parts, which are the anterior and posterior sense-organs respectively. The auditory vesicle is at the same time partly separated into two chambers (incomplete canals) to accommodate them. These chambers are the utriculus and sacculus.

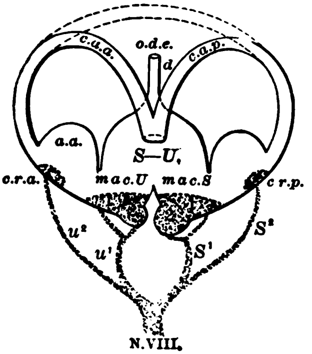

FIG. 15.— The Cyclostome type ear shown here is a very simple structure as compared with the complicated organ found among the *Gnathostomata*, but compared with its ancestral condition, *i.e.* the auditory vesicle, it is seen to have gone through many changes, and stands to-day midway between its earliest condition and the highest differentiation known. This diagram is constructed on the basis of the anatomy of the only two known forms of this group, *Myxine* and *Petromyzon*. The canals and their organs retain a very primitive condition of structure.

caa	Anterior canal.
cap	Posterior canal.
cr. a	Crista acustica anterior.
cr. p	Crista acustica posterior.
d	Endolymphatic duct.
u.s	The utriculo-sacculus.
u 1 and 2	Branchlets of the utricular branch of the auditory nerve.
s 1 and 2	The saccular branches of the same.
ode	Terminal portion of the endolymphatic duct, which in neither of these Cyclostomes opens on the surface of the body in adult life.
mac. u	Macula acustica utriculi.
mac. s	Macula acustica sacculi.
1 and 2	The portions (1) of the sense-organs that remain in the parent cavity and the portion (2) which migrate into the recessus utriculi and **lagena** respectively.

Each of the two sense-organs of the second generation after a while divides into two unequal parts in such a manner that the smaller sense-organ appears as a bud from the parent. There are thus formed within the two chambers of the ear four canal sense-organs belonging to the third generation. The two external organs are soon enclosed within the ampulla of two complete and relatively large canals, which are now formed about them. An anterior vertical and a posterior vertical formed in the manner already fully described. Up to this time the organs have retained the primitive relations to each other — a serial arrangement along a line running in an antero-posterior direction. Now, there begins a distortion of the structure as a whole, which continues ever after, and reaches its greatest development in the mammals — viz. a process of sinking and drawing out ventrally of the posterior chamber of the ear, so that hereafter we might speak of a superior and an inferior portions or chambers. The sense-organs of the third generation play the leading *role* in these changes, and by means of four sets of divisions, viz. by the bipartition of each sense-organ present in the Cyclostome stage nearly simultaneously there is produced a fourth generation of canal sense-organs.

To this fourth generation belong all the sense-organs of the internal ear of the higher vertebrates which in the diagram are numbered eight to fifteen consecutively.

During this process of sense-organ differentiation, the canals have been variously modified, and to show the relationship of the third generation to the fourth let us examine the diagram shown in Fig. 15, in the construction of which I have ignored the ventral distortion spoken of.

The sense-organ numbered six in the Cyclostome stage (the crista acustica anterior, or anterior canal organ, of *Myxine* and *Petromyzon*) has divided to produce sense-organs ten and twelve of the Gnathostome stage, *i.e.* the cristæ acusticæ anterior et horizontalis, of the human ear.

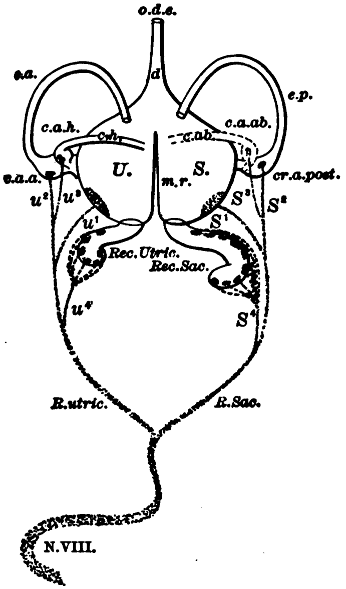

FIG. 16.—The Gnathostome type ear shown here illustrates the method and the extent of the modifications which the Cyclostome ear has suffered in its descent to this group. The anterior and posterior canal organs have each budded off an organ which, in the case of the anterior canal, produces a well-formed canal, the external, present in all the members of this group, while the posterior bud never produces a well-formed canal. The utricular recess, which contains a number of sense-organs derived from the division of the macula utriculi, is represented as forming a tubular prolongation of the utricular cavity, in order to more clearly show the parallelism of this group of organs with the lagenar group. In no known form does the production of the canal proceed to the extent shown in the diagram. The sense-organs of the lagenar group are represented as separated from each other by an interval, whereas the actual relation in nature is much more intimate.

ca	Anterior canal.	*rec. utric*	Recessus utriculi.
cp	Posterior canal.	*rec. sac*	Recessus sacculi.
ch	External canal.	*d*	Ductus endolymphaticus.
c. ab	Abortive canal.	*s*	Sacculus.
u	Utriculus.	*o. de*	Orifice of the same.

The sense-organ numbered four of the Cyclostome stage (the macula utriculi of *Myxine* and *Petromyzon*) divides into the sense-organ eight and sense-organ complex fourteen of the Gnathostome stage, the macula utriculi of the human ear, which is, as I stated when describing the Torpedo ear, a compound organ composed of the parent organ and its numerous progeny, all of which remain close together.

The sense-organ numbered seven of the Cyclostome stage is the sense-organ of the posterior canal of *Myxine* and *Petromyzon*, and has divided to produce sense-organs, eleven and thirteen, of the Gnathostome stage, or the crista acustica posterior, or the canal sense-organ of the posterior canal of the human ear, and the so-called *macula acustica neglecta* of Retzius, which is the abortive second horizontal canal organ of the internal ear of man.

Sense-organ five of the Cyclostome stage has divided to produce the sense-organ nine, and the sense-organ complex fifteen of the Gnathostome stage, or the macula sacculi and the lagenar organ respectively, the organ of Corti of the human ear.

With the exception of the generalization that the vertebrate internal ear is derived from branchial sense-organs — *i.e.* organs of the lateral line system — a generalization which we owe to Beard, but which he did not attempt to establish by any detailed anatomical or embryological investigations, the phylogenesis of the vertebrate ear has been studied only on the basis of the adult structure. Such structures as the semicircular canals and the divisions of the body of the auditory vesicle have been used alone as the basis for proofs of the genetic connection of the types of internal ear — even the nerve supply has been excluded from its just share in forming the conclusions.

These canal structures had no special phylogenetic significance for investigators in this field; for although it was known that the auditory vesicle was invaginated from the surface of the body, the connection of the sensory part of the invagination with the superficial canal organs was not understood. Now that we know that there is a genetic connection, many of the intricate problems receive their solutions, and the genetic relationships appear clear and certain for all the types. The demonstration of these facts deals another blow, and a fatal one, at the degeneration hypothesis which has been so persistently applied to the elucidation of Cyclostome anatomy and development, with such pernicious morphological results. (This will apply equally to Amphioxus, though only indirectly in this particular instance.) This solution relieves us from the necessity of explaining away the vertebrate ear on every occasion, when we seek to establish a relationship between the vertebrate and the invertebrate types; for we are led to see the value of very simple, superficial, sense-organs in an undifferentiated group of animals, for the building up of structures of great complexity, and of intricate relations to other parts of the animal body in the members of higher forms, and also to recognize the manner in which the structure and functions of organs may be profoundly changed in the course of time.

Now, while it is not known that Amphioxus is provided with an organ of hearing, the next higher forms do possess an internal ear of such structure that not only does it help us to understand the more complex

Gnathostome type, but proves conclusively that, so far as the ear is concerned, the Cyclostomes have not suffered degradation of structure.

Against the view that the completely closed or perfect canal is the primitive condition of this system, *so far as existing vertebrates are concerned*, one may raise the very plausible objection that since all the Holocephala and some Teleosts have the canal incompletely developed, as a more or less open groove on the surface of the body, and since the Cyclostomes do not retain the superficial canals except in very imperfect form during adult life, and further, since the closed canal is produced in ontogeny, and may have appeared in phylogenetic history by the action of the same process,[1] it is only reasonable to suppose that the open groove is the primitive condition, and constitutes a phylogenetic stage passed through in the development of the *higher* (?) types of closed canal.

When, however, we consider that the internal ear is a very ancient structure, and that in all known cases the sense-organs developed in it become enclosed in *complete* canals, by a process exactly similar to that known for the formation of the superficial canal organs and their canals in the admittedly primitive ganoid type, we are compelled to admit that such a process could hardly have arisen independently within the closed capsule after its separation from the surface and its removal away from the external influences which originally caused their development, and that consequently *there*

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[1] *e.g.* the grooves present on the surface of the head and body of *Chimæra* and *Tetrodons*, could readily be converted into tubes by the fusion of their edges.

must be a genetic relationship between the canal organs of the internal ear and the superficial canal organs; and since there is not the slightest doubt that the superficial canal organs are the original or parent organs, we are brought to the unavoidable conclusion that *the vertebrate internal ear is a transformed canal organ.*

It follows from what I have said that the system of canal sense-organs must be a *very* ancient one, since it must have antedated the origin of the internal ear of the Cyclostomes.

Although *ontogenetic* evidence seems to lead to the conclusion that the auditory organ arose by the invagination of *a single superficial sense-organ*, it is by no means certain that this is true; for there are certain facts of comparative anatomy and certain phylogenetic considerations which point to the conclusion that the auditory organ has arisen by the bringing together of two originally distinct sense-organs which were together sunk below the surface. The main facts at present in favor of this view are these:—

1. In all eared vertebrates the auditory organ is supplied from two distinct brain centres, one lying in close connection with the facial nuclei, the other intimately related with the glossopharyngeal nucleus.

2. In all eared vertebrates the so-called auditory nerve is composed of two distinct roots—an anterior and a posterior—which supply the anterior and posterior chambers respectively.

3. In all these forms the anterior root is external to the brain, united with the facial nerve.

4. In some fishes the nerve to the posterior ampulla is derived from the glossopharyngeal nerve, between

which nerve and the posterior root of the auditory there exists, however, a more proximal connection.

5. The auditory vesicle is always developed between the facial and glossopharyngeal nerve roots.

6. The ductus endolymphaticus is supplied on its anterior face by a branch of the utricular nerve, while its distal end, in some fishes, opens into a canal containing sense-organs innervated by the glossopharyngeal nerve.

7. The so-called eighth cranial or the auditory nerve must have arisen from branches of two distinct cranial nerves, and is not homodynamous with such cranial nerves as the fifth or tenth, as we now understand them. This is true (*a*) because the auditory sense-organs thus supplied were primarily only a portion of the canal sense-organs innervated by the original nerves of the preauditory condition of these sense-organs; (*b*) because the auditory nerve is clearly not a complete nerve, and is not even equivalent to a dorsal root of a cranial nerve, for its two divisions are probably merely branches of the dorsal roots of the seventh and ninth nerves, since they draw off only a portion of the sensory fibres from these two nerves.

The primitive division of the auditory chamber and its nerve supply into two so sharply marked portions is thus phylogenetically accounted for, and at the same time the early ontogenetic changes in the auditory vesicle receive their explanation.

The two sense-organs, the maculæ acusticæ of the utriculus and sacculus, are thus derived from two organs terminating two separate canal systems which had, as they may still be seen in *Amia*, become confluent on the surface of the body midway between the roots of the facial and glossopharyngeal nerves as they issue from the brain. At the point of junction the two half-pores united into a single pore, which in some fish forms (*e.g.* Torpedo) persists as the outer opening of the endolymphatic duct, and the only persisting indication of the separate origin of these organs and their canals is their nerve supply. It is a necessary consequence of the great functional differentiation which the ear organs have suffered that their nerves should also become much increased in size, and instead of appearing now as *nerve branches* they have become really larger than the parent nerves from which they arose.

As a prelude to the little I have to say on the physiology of the internal ear, I wish to emphasize the following considerations: We have very slender foundation indeed for correctly judging of the functional relations of the integral parts of the internal ear, and what we have is largely speculative, based on our knowledge of the structure of the parts.

What we need at the present time is physiological experimentation. First of all, an extended series of varied, careful, and unbiassed experiments on the sense-organs of the lateral line system of the lower vertebrates, to determine their functions, and then more experiments on the internal ear of the least differentiated representatives of our type, to determine what functional modifications have arisen during the transformation processes. Finally, the combination of the knowledge thus gained, with the results of experiments upon the human subject.

If proof were needed for the statement that most of the speculation and experimentation on the auditory function, especially as regards its different phases, has led mostly to negative results, it is easily forthcoming; for there is not a single investigator who, during the last half-century has written on this subject, but regrets the paucity of facts and the depressing insufficiency of the prevailing theories.

The amount of experimental knowledge of the functions of the lateral line organs is very limited indeed. Of the many theories which have been proposed Merkel's is by far the most satisfactory. According to this investigator, the function of these organs is in all probability that of receiving and transforming the *mechanical* stimuli occurring in the surrounding medium, and it annot be in any way connected with the perception f *chemical* changes in the water.

Mayser and Emery consider the organs of the lateral ne system as forming an accessory auditory organ, d Mayser has proved that these organs find their ntral brain connections in the immediate neighborod of the auditory nuclei.

The functions of the ear are usually separated o two classes by physiologists. The first and st prominent of which is AUDITION, with its several divisions; the second, though less prominent, not that reason, however, less important, viz. equilibra-

The function of audition certainly belongs to ear; not so, however the equilibrious function; t can be conclusively shown that equilibration t necessarily affected by the removal of the ear, that injury to other organs is not unfrequently followed by loss of the ability to equilibrate the body.

An extended presentation of the arguments for and against the equilibration theory of the semicircular canals would be too long and unprofitable to justify introducing it here, especially so now that there is no longer the slightest evidence in favor of the theory, since the results of experiments by the physiologist Steiner have been published. It is commonly stated that the auditory nerve, besides possessing the function of transmitting auditory impressions, also transmits stimuli to the equilibrious centre, and that the ampullæ of the semicircular canals contain the sense-organs which subserve this function.

The ampullar sense-organs may, however, be completely severed from their respective nerves without producing any disturbance in the equipoise of the body. The section of the ampullar nerves, even though the greatest care be taken to prevent damage to the connecting nerves, must produce an intense stimulation of the central end cells, and it is wholly unexplained why the ampullar nerves may be thus cut without producing any visible effect if the equilibration theory were true.

Experiments carried out in Hermann's laboratory in 1877, by Fraulein Tomaszewicz, showed that in bony fishes the semicircular canals and their ampullary sense-organs could be entirely removed without in the least influencing the equilibration of the body. Another set of experiments, even more decisive, were performed by Professor Steiner in 1888, in the physiological department of the Naples zoological station, on the common Dog-fish of the Bay of Naples. Steiner's experiments proved that so long as the fibres of the acoustic nerve were neither pulled so as to disturb their central relations, nor displaced in a manner injurious to their peripheral terminations, disturbances in the equilibrium of the body did not make their appearance. While observing these conditions it was possible for him to cut out one, several, or *all six of the semicircular canals without destroying or in the least disturbing the fish's power to equilibrate its body,* though the operation evidently caused the fish very painful sensations, *i.e.* very intense irritation of central end cells.

Now under the old hypothesis of the equilibration functions of the semicircular canals, these removals without equilibrative disturbances would be impossible. Experiments of a similar nature performed on warm-blooded animals were formerly used as evidence in proof of the theory. In all of these experiments disturbances of the power of equilibration never failed to make their appearance. These disturbances, however, were due to the conditions under which the experiments on warm-blooded animals are necessarily performed, and are not directly related to the injury to the nerve from simple cutting. In Pigeons whose semicircular canals have been more or less injured[1] or destroyed, the loss of coördinating power is certainly to be connected with the injury done to the richly nervous structures; but it does not follow that this loss of coördination is due solely to the disturbance of the function of the canals, for it can be clearly shown that during the wounded state the bird is still able to equilibrate itself under certain conditions, and those conditions involve calling into use the tactile sense. The sensation of giddiness produced by injury to or destruction of the canals is due not to the injury of the ampullar sense-organs, but either to a disturbance of the centre of equilibration in the brain by mechanical injury to the cells of this centre, or to the cessation of the perceptions arising in part from the functional activity of the auditory mechanism. It has been observed that a pigeon operated on by canal section or destruction can, and usually does, steady itself and properly direct and execute coördinated movements, the moment its sense of sight is aided by the tactile sense sufficiently to enable it to form a correct judgment of its position in space and its relation to surrounding objects.

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[1] As in the experiments by Elourens, Cyon, and others.

Now, barring nausea or other nervous disturbance accompanying section among the warm-blooded animals, it is plainly true that the animal's failure to coördinate its movements lies in the fact that it forms false judgments of its spacial relations on an insufficient basis sense-perception, the constant stream of auditory impressions having been cut off, even in the milder experiments, by the disturbance of the pressure equilibrium of the endolymphatic fluid.

On the basis of the evidence which had been produced by the advocates of this doctrine, Milne-Edwards disposed of the kinetic and statical theories of the equilibration functions of the semicircular canals in the following words: "Mais les hypotheses proposées à ce sujet ne reposent pas sur des bases suffisantes pour que nous y arrêtions ici."

Audition is the resultant of all the wave motions, transformed and transmitted to the auditory centre in the brain by the fibres of the auditory nerve.

There are several kinds or conditions of auditory stimuli, depending, first, on the *intensity* or force of sound (*i.e.* the amplitude of vibration); second, on the pitch of sound (*i.e.* the number of vibrations in a given unit of time); and third, the quality or timbre (*i.e.* the result of the form of the sound wave). Upon the combination of these conditions, in varying proportions as they occur, depend the character of the auditory impressions.

The variability in the powers of auditory perception among animals is much greater than is commonly supposed. As instances of increased sensitiveness above that of the human ear one may mention mice, cats, and other nocturnal animals. Galton found that the house cat among domestic animals possessed a wonderful capacity to perceive shrill tones, and it is a common experience that the cat's ear is super-sensitive to auditory stimuli.

All vertebrates above the fishes are provided, like man, with a tympanic membrane and a chain of bones, or its functional equivalent, which serve to transmit vibrations to the internal ear; but while we are accustomed to look upon this arrangement of the parts as presenting us with a greater perfection of the auditory apparatus than is present in the lower forms, it is not by any means proven that such is the case, for this accessory apparatus is a ponderous mass, which only relatively powerful vibrations can set in motion. All vibrations of the air which do not succeed in moving this conducting apparatus are lost to us. It is for the purpose of making up this great loss that the external ear has been developed. Traces of accessory apparatus to place the internal ear in more favorable communication with the exterior, begin to make their appearance among the cartilaginous fishes, whose ears still retain their direct connection with the sea-water by means of an endolymphatic duct. This tendency is due to

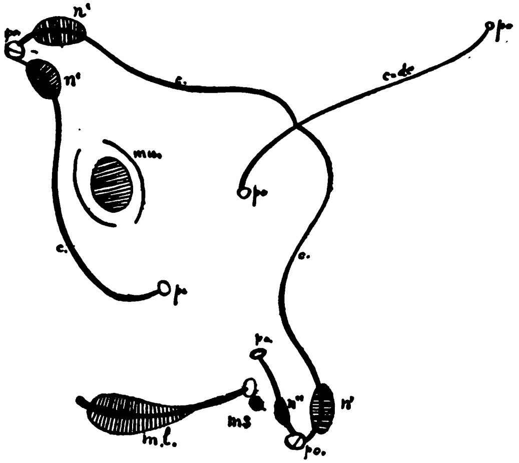

FIG. 17.—A projection of the internal ear on a flat surface, to illustrate the relations of the sense-organs and canals of the Torpedo ear, when the auditory chamber is brought to the surface and spread out flat.

c	Canal.	*n''*	Macula neglecta.
po	Canal pore.	*ml*	Papilla lagenæ.
n'	Crista acustica.	*ms*	Macula sacculi.
mu	Macula utriculi.	*c. de*	Endolymphatic duct.

the removal of the ear from the surface of the body, and is greatly increased as soon as the forms emerge into the poorer conducting medium of the aërial ocean.

When the structure of the internal ear of the higher vertebrate has been analyzed with reference to determining its functions, we find that it is easily reduced to the type of the canal organ on the surface of the body, and we should expect an essential harmony between the functions of these two groups of organs, although in the case of the ear the functions would necessarily be in some degree modified to correspond with its modifications of structure. These latter, we know, have not been extensive, except in the case of the cochlea, and, strange as it may seem, we are not able to assign to the cochlea any function at all in keeping with the great complication of structure which it has undergone during its evolution from the lagena.

The Helmholtz piano-string theory is entirely inadequate to account for perception of musical tones by vertebrate animals, in that it can be applied only to the higher mammalian forms, and leaves us to seek another explanation for the equal, if not greater, powers of musical perception possessed by some birds. Whatever explanation future investigation may disclose to us, it is safe to say that it will prove equally applicable to all vertebrate forms capable of musical perception, while being in perfect harmony with the then perfected knowledge of sound (tone) perception by means of lateral line organs.

In closing, allow me to recapitulate the more important features of oto-phylogeny, past, present, and to come.

In the PAST the ear of man was a canal organ of the lateral line system of sense-organs. A system which has disappeared from the surface of the adult human body; but which still occurs in a reduced condition during embryonic development. All its organs regularly produced protective canals, and the auditory organ came to differ from the neighboring organs merely in size and the greater depth of its ampullar pit. At first its functions were identical with those organs of the same system, having the same nerve supply; but as it was more and more removed from the surface of the body, it acquired greater protection against injuries and concomitantly greater sensitiveness. It increased in size and began the process of division, which has resulted in the organ as it exists at the present day.

These changes required untold millions of years for their perfection; for, since palæontological science tells us that this same Amia or ganoid Dog-fish which has retained its surface organs in such a primitive condition, existed in its present form, at the very least, twelve millions of years ago, you will readily conclude that the human mind can form no adequate conception of the period of time which elapsed since the ancestors of the Dog-fish were like the Cyclostome fishes in the structure of their ears.

For we know that at the present time Amia has an internal ear of greater complication than the Torpedo, which I briefly described to you at the beginning of the hour. The auditory organ has played a long and very important rôle in the phylogenetic history of man. The auditory organ of man has no genetic connection with any of the invertebrate auditory structures.

At the PRESENT time the human ear is a canal organ complexus, constructed according to a simple and symmetrical plan, whose ontogenetic history is a recapitulation of many of the stages of its phylogeny. During its development it is badly distorted, and the simplicity and symmetry of the plan of its construction is thus in a measure concealed. In its adult condition it is not the most highly differentiated ear known to us, for some other mammals are far more fortunate in this respect. It is an organ about whose functions we know little, since most of what is written in the text-books is pure speculation, much of which is proven to be without foundation, if, indeed, it is not directly controverted by recent experiments.

It subserves the auditory function, and has no more to do with the equilibration of the body than many other organs, especially those of the higher senses. Its canals are not organs of equilibration.

The FUTURE of the human ear can only be foreseen in terms of its past and present. It will probably develop functionally much more than structurally. Its semicircular canals will gradually undergo reduction, while its utricular and saccular complexes of sense-organs will increase in size and perfection of structural detail, in response to the increasing demands for tonal differentiation; it will, nevertheless, remain in the human descendants of the distant future, whatever their form may be, however keen or diversified their auditory function may become, merely **A TRANSFORMED CANAL ORGAN.**